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The Structure of Cereal Straws

By FRANCIS E. LLOYD, F.R.S.C. McGill University.

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General Summary.

In the following paper, the results of a study of the structure of the four principal cereal straws have been given. The purpose of this study was to determine (a) the major differences in structure, especially as to the character and length of the fiber, and (b) the possibility of distinguishing the elements (cells) of each in a macerated product, or in a straw paper.

In view of the variability and overlapping of characters the latter task is not an easy one. The present attempt was of necessity confined to samples of four cereal straws supplied to the author. These embraced only one race, doubtless an impure one, of each kind. The findings were, however, checked by comparison with pure, strain material (or nearly pure), with the result that it became necessary to revise some of the conclusions. This teaches that a thoroughgoing study of this sort must embrace a large array of materials, failing which the results must of necessity be to some extent equivocal, and subject to revision. With this admission, we are however permitted to say that it is possible by careful inquiry, to determine the origin of the materials in a given straw paper, or other straw-product, with considerable certainty.

Whatever the limitations, however, of this study, it will serve to bring forward a basis for future ones in the same field without being negligible with respect of the amount and character of the information it contains, which, in both regards, is certainly in measureable advance of the present available. The latter is both meagre in quantity and often inaccurate in character.

It is the purpose of the present paper to give an account of the structure of the "straw" of the barley (*Hordeum*), oat (*Avena*), rye (*Secale*), and wheat (*Triticum*), based upon specimens from single localities and of ordinary ripeness, or degree of development (1). It will be understood that minor structural differences, such as characterize various races of these cereals, and even a single race grown in different localities, are beyond our scope. Such differences may well have to be considered in the event that the straw is to be used for special purposes, but in any event they would have to be investigated in relation to such purposes.

It is further important that the structure of the straws of grasses shall be well enough understood so that it is possible to distinguish the origin of the structural elements as they may be found in materials, such as paper, manufactured therefrom; for it is easily possible that litigation may arise requiring such special knowledge in its settlement. That this task is by no means easy was the opinion of Wiesner (1910), who has given much attention to the general subject of paper materials. His conclusions, which indicate the difficulties in some detail, are more specifically mentioned beyond. It is believed that the evidence presented in this paper is such as to show that Wiesner was not wholly justified.

(1) The specimens were supplied by Arthur D. Little, Ltd., who also bore the major expense of the preparation of this work. The co-operation of the Forest Products Laboratory, especially through the valued assistance of Mr. W. B. Stokes in the preparation of negatives herein used, is heartily acknowledged. Mr. G. G. Moe collected material for comparison at the Experimental Farm, Ottawa.

What is "Straw?"

By "straw" is meant the stems of mature cereals and the remnants of various structures, especially of leaves which may remain attached thereto. The term is also extended to similar plants, such as esparto, when collected for use. "Hay" is the same thing, but is cut before maturity, so that there is a much larger amount of food material in the stems and leaves, which are at the same time less indurated, and in the immature grain (seed). When cereals are cut as hay, the unripe grain is left attached—barley hay, for example,—thus increasing the food value.

The straw that is obtained by machine threshing is always more or less broken, and in any event the leaves are shrivelled and more frequently torn away than otherwise. Owing to the peculiar structure of the leaves however, a part, namely the *leaf-sheath,* remains rather tenaciously, as will be seen later.

In reaping, the stems are cut off at about six inches from the surface of the soil. About this length of stem is therefore left behind, together with the parts (stems and roots) which lie on or below the soil surface. In this study, excepting only certain measurements of stature, these parts are disregarded, since they do not enter into any consideration of the usefulness of straw as such.

The Natural Affinities of the Cereals.

The cereals or grain plants belong to a large and universally distributed group of plants known as the grasses (*Gramineae*). It need hardly be said that these plants are of fundamental economic importance, primarily as food, and secondarily in manufacture. In addition to our own familiar grains, rice (*Oryza sativa L.*) may be mentioned as of an importance as a food supply equal to, if not greater than, all the other cereals taken together, as a present economic fact. Indian corn, or maize (*Zea mays*), sorghum, Kaffir corn ("durrha") and sugar cane are other well known examples of prime importance. In the Orient, young shoots of the bamboo are used as a vegetable. A very great variety of grasses furnish grazing and hay, thus adding to a grand totality of usefulness, which is discounted but little by the fact that a very few grasses are poisonous. More than usually interesting in this connection is the fact that ergot, a highly poisonous but therapeutically useful product of grains, is the hypertrophied grain (especially of rye), caused by the presence of a fungus parasite, (*Claviceps purpurea*).

Of possibly great economic importance in Canada is the wild-rice (*Zizania* spp.) which furnished a staple food for the Indians, and which offers an opportunity for extending cultivation to lands which cannot be drained sufficiently for other agricultural purposes.

As to other uses, the grasses furnish material for a variety of purposes ranging from building to personal adornment. In the tropical regions are found the giants of the host, the bamboos, which more especially in the Orient grow to large sizes (70 feet tall) in many cases, and furnish an amazing variety of materials for use in building, boat building, furniture making, and in the making of an endless variety of smaller articles. The

straw from the heads of sorghum (broom-corn) is used in the manufacture of brooms and brushes.

The mechanical qualities which fix the value of the material for these purposes are strength, lightness and springiness which combined are exemplified in the highest degree in the split bamboo fishing rod. Even ordinary straw of common grains shows these qualities in a remarkable degree, relatively to the amount of material in it. One needs but to recall the lightness and stiffness of a lemonade straw — now largely supplanted by imitation straws made of paper and paraffine — to realize this.

The Structure of the Straw in General; Gross External Structure.

As has been indicated, straw consists of two parts, the stem and the attached leaves. The stem is composed of straight stretches of approximately cylindrical shape and various lengths, the *internodes*, articulated at the *nodes*. Properly speaking the node is merely the transverse region of the stem from which arises a leaf. In the grasses, however, the base of the leaf is usually swollen, forming a prominent band (motile organ) about the base of the succeeding internode (figure 1). In the dried straw this swollen collar is shrunken, and presents characters which enables one to distinguish between the kinds of straw here under consideration in some degree.

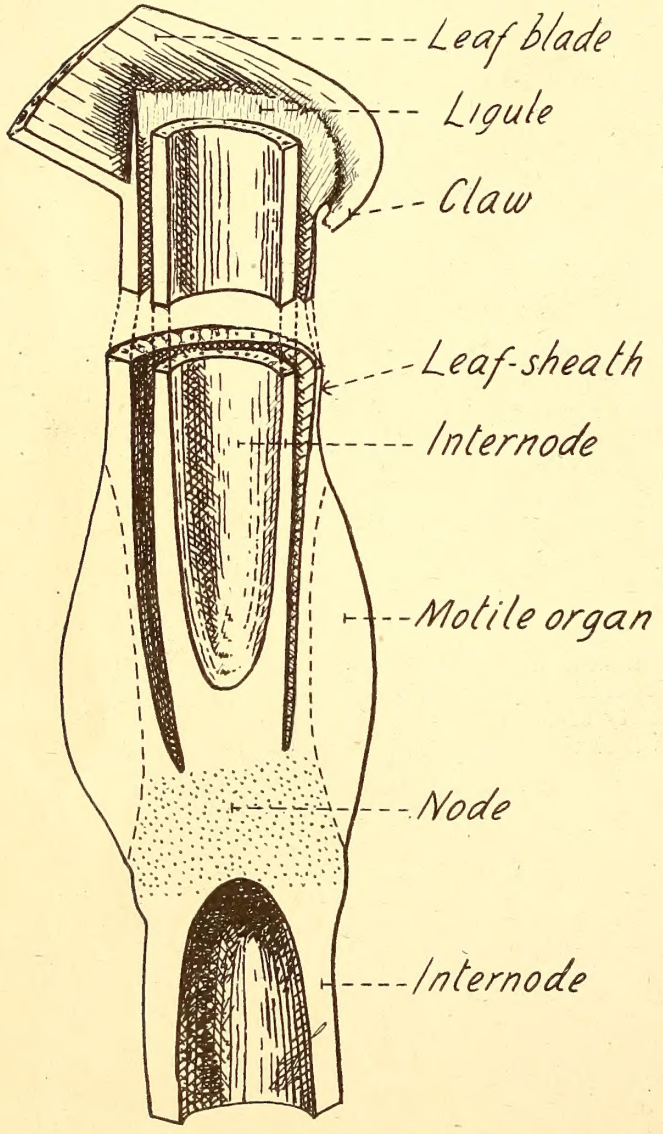

Fig. 1. — Longitudinal sections through a node of wheat straw. The broken lines indicate the shape of the leaf base (false node) when dry and shranken.

The leaf is composed of two parts, the leaf-sheath and the blade. The leaf-sheath is the lower portion which springs from the node and folds about the internode above. At the top of the sheath the blade springs away from the stem, and at this point is found a membranous projection which clasps the stem apparently as a continuation of the sheath, known as the ligule (figure 1, 29). The edges of the blade sometimes project, clasping the stem (figure 28). The projections are called auricles or, more simply, *claws*. The size, shape and other features of this organ serve as distinguishing marks for identification, which, in the absence of the grain and its accompanying parts, are relatively of great use in the recognition of the kind of straw (Carrier, 1917).

At the base of the blade there is always a more or less conspicuous transverse zone, the *collar*, having, when well developed, much the same structure as that found in the swollen base of the leaf sheath, (as *e.g.* in orchard grass). When inconspicuous, as is the case in the grains here to be considered, the collar is indicated only by a more or less evident thickening of the veins as they traverse it. The collar is a motile organ analogous to the swollen leaf sheath base, and at this point the blade bends into a position approximately at right angles to the axis of the plant.

The swollen leaf bases, which may here be called *false nodes* for the lack of a better term, are important organs by which the growing grass shoot maintains its upright position. Should young grain be "lodged", the upper portion of the stem will readily regain a vertical position, and on examination it will be found that the requisite bending has been confined wholly to the false node and the ensheathed base of the included internode, as evidenced by the unequal development of the false node on the upper and lower sides. It is only rarely that the lower parts of straw do not show more or less bending. The false nodes and leaf sheaths, incidentally, help to distribute the strains imparted to the straw by bending, as e.g. under a heavy wind, so that the breaking of the stem at the base of an internode is usually obviated. This view of the mechanics of the grass straw has been denied, but without good reason. As a matter of fact the younger tissues of the internode are at the base, and the weight of the parts above could not be successfully supported during development were it not for the leaf-sheaths. This is very obvious in growing corn (maize). In the dead, dry straws the false nodes very obviously form supporting bands, strengthening the shaft at these points. To be sure the tissues are in this condition hard and indurated, while in life they are much softer and more pliable. In any event, however the mechanical value of the false node is but contributory, while its primary function is that of a motile organ, as above explained.

The leaf in the grasses is always conspicuously ribbed and veined, the veins running parallel, except for their gradual convergence toward the apex, and the same is true of the stem, except at the nodes, where the veins branch and redistribute themselves into the leaf and next node above (2). In harmony with the anatomical scheme underlying the structure of grasses, there is an evident elongation of most of the external and internal structures.

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(2) This topic is apart from the present purpose, and hence will not be further mentioned. Those interested may consult Chrysler, 1906.

Gross Internal Structure.

In most grasses the stem, excepting at the nodes, is a hollow cylinder of almost geometrical regularity. The exceptions in which the stem is a solid mass of tissue are, conspicuously, the sugar cane, Indian corn and a few others. The hollow joints of bamboo, used as flower holders, and in the tropics as water holders, flowerpots, etc., are familiar examples of the hollow structure; still more so the lemonade straw.

As a mechanism possessing the maximum strength relatively to a minimum amount of material it approaches perfection, that characterizing the hollow column. Owing to the properties of the materials, which have a high modulus of bending, the column is not easily broken even under a transverse strain. The terminal internodes of the rye serves as an excellent example. One 55 cm. long, 0.7 mm. in diameter at the upper end, and 1.2 mm. at the thickest point and weighing only 0.25 grams could support 5 grams when supported 10 cm. from the base, with bending through an arc of 15 degrees in the dry condition. The walls of the cylinder were only 0.2 mm. thick. It is of course only when the strength available comes within the ordinary range of necessity that grass stems become useful for the inherent mechanical properties, the bamboos being in this regard notably efficient. Even grain straws however, meet special needs, but aside from ordinary experience.

Each internode tapers slightly towards the base, and is generally somewhat constricted just below the node. The terminal internode however tapers gradually from its thickest part, which is nearer the base, to the ear (inflorescence). The entire upright stem, or straw, consists of three to four internodes in barley, oats and rye, in wheat three, excluding the shorter internodes which occur within 6 inches of the ground. The differences in the length of straw are due chiefly to differences in the length of the internodes, and less to their numbers. The relative lengths and total lengths, based on the measurement of ten straws of each grain are shown in the table. (figure 2.)

TABLE.

Species	Total length of straw	Length of internodes				
		Top	2	3	4	5
	cm.	cm.	cm.	cm.	cm.	cm.
Barley	56	28	17	8	3	..
Oat	91	49	24	16	2	..
Rye	149	53	46	28	12	10
Wheat	69	42	22	5	..	..

The measurements for the bottom internodes in the above samples are however only partial, since in reaping, a basal portion of the straw is left. Measurements of complete straws based on samples grown at MacDonald College, and at Ottawa, in pure, or nearly pure cultures, gave the following measurements:

	Total	Top	2	3	4	5	6	7
Barley—								
"Chevalier" . . .	79	26	19	12	10	6	3	3
	103	34	24	17	14	10	4	..
Oats—								
"50 lb. Black" . . .	81	41	17	11	7	4	1	..
"Banner"	84	41	17	13	8	4	1	..
"Alaska, 712" . . .	95	41	22	15	9	6	2	..
"Banner"	98	42	20	15	10	7	4	..
Rye—								
Common	111	42	32	21	13	6	2	..
	112	39	32	20	13	6	2	..
Wheat—								
"Marquis"	104	50	21	11	8	4	..	..
"Marquis"	93	52	21	11	7	2	..	..
"Red Fife" . . .	105	58	23	12	8	4	..	..
"Pringles's Champ"	84	50	17	9	6	2	..	..

It is evident that, due to both racial characters and to "place effect" it would not be easy to identify the grains merely by casual measurements of the straws. Nevertheless certain features emerge from the above figures which serve as a guide of some value, especially in the relative lengths of the uppermost internodes. For example, the terminal internode in wheat is 50 per cent. of the whole straw in length, and over twice that of the sub-terminal internode. Similar comparisons bring out equally useful ratios, but it is unnecessary here to discuss them further. We may say however that it would be possible, given the samples of straw, to fix upon the grain with fair certainty by such measurements as these alone, and in conjunction with other measurements, to arrive at practical certainty.

We note that wheat has one less internode in the straw than the others. About one in ten rye straws

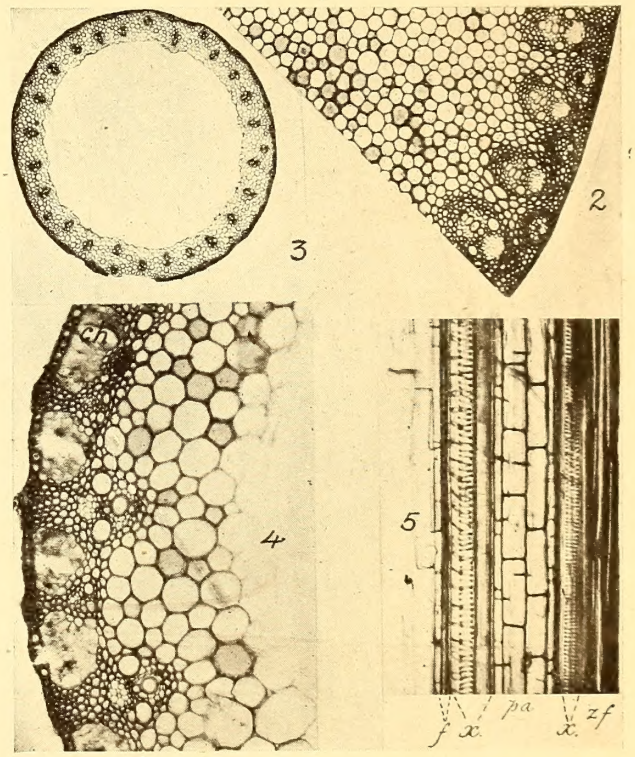

Figure 2. — Sector of a transverse section of a wheat stem taken just above a node, where the fistula is not developed, and the stem therefore solid. × 65.

Figure 3. — Transverse section through an internode of barley, showing the fistula, and the bundles in the parenchyma. × 6.8.

Figure 4. — Sector of a transverse section through the upper part of the terminal internode of wheat. The fiber layer is interrupted by the chlorenchyma spaces (Ch) which underlay the stomatal zones in the epidermis. × 97.

Figure 5. — A longitudinal section of the stem of barley. The fiber layer (zf) appears quite dark on account of the small diameters of the cell lumina. The ring and spiral thickenings of the wood of two bundles (x) can be well seen. A secondary series of wood vessels can be seen on the right of the annular vessels of the left hand bundle. × 65. pa. parenchyma; f. fibers.

shows part of a seventh internode. The thickness of the various straws bears no relation to the stature.

A conspicuous feature of the grass stem and leaf already referred to is the fine longitudinal ribbing and alternate "fluting", especially obvious in straw which still shows the green color, though it can be seen quite readily by the deep yellow color after the green has faded away. This appearance is due partly to the presence of low longitudinal ridges, and partly to the structure underlying the outer tissue, the epidermis. This relation will be made clear later.

Anatomical Structure.

A glance through the microscope at a bit of straw, however prepared. will show at once that the mass is made up of a large number of small units, each composed of a wall enclosing a space which may be either empty or contain the remnants of various substances which were important during the life of the plant. It is convenient to designate these units by the term cells, as originally used. (4)

Structural groupings of cells of similar size and shape are called tissues. In the immediately following paragraphs the form and dispositions of the cells and tissues will be described. It will be convenient to begin by examining the structure of a stem as seen in transverse sections.

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(4) "Cell" was used by Robert Hooke in 1665 for the cavities seen in cork. The term has now a more fundamental significance, being applied to the living matter which, in plants, builds up a cellulose skeleton by which the form of the plant is maintained. There is no living matter present in "straw", which is merely the relatively indestructible skeleton of the erstwhile live plant.

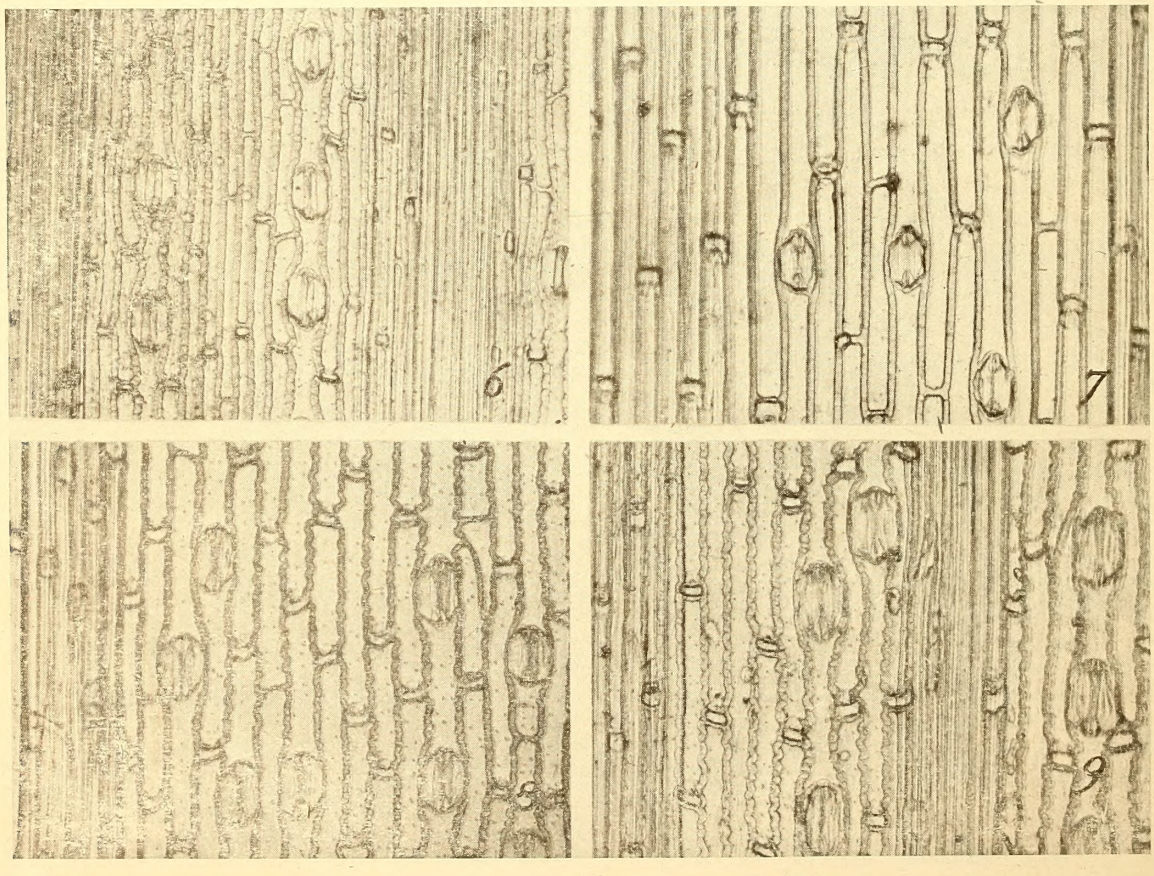
THE STEM.

If such a section is taken just above the node, where the stem is not hollow, the following structure will be seen (figure 2).

The section is nearly circular, and appears made up of a mass of round cells constituting the parenchyma, the largest in the middle, and grading in size toward the edge when they meet with a much denser lot of tissues. These are evidently arranged in groups of cells (the fibro-vascular bundles) of different sizes, between which the parenchyma extends toward the periphery of the section. There are apparently two, but strictly speaking more than two, circular series of fibro-vascular bundles, the inner of larger ones, and an outer of smaller ones, paced quite close to the surface of the stem. Between the bundles of the outer series the cells are very small, and as will be seen, make up a layer of fibers (bast). (*cf.*) figure 5).

Bounding the whole is a single layer of cells of small size and approximately quadrangular in transverse section constituting the epidermis. On comparing with a section (figure 3) from a somewhat higher level in the internode where the stem is hollow and where the tissue arrangement is best displayed, it will be seen that here the structure differs from that just at or above the node chiefly in the circumstance that the parenchyma in the middle has broken down thus leaving the space (fistula). At a still higher level it is seen that there may be an interruption of the dense mass of small-celled tissue just beneath the epidermis, by stretches occupied by very thin walled and loosely arranged cells (the chlorenchyma) which, when the plant is alive, contain the green coloring matter (figure 4).

If now a section running lengthwise the stem is



Figures 6-9. — The epidermis viewed en face of the stem (upper part of a lower internode) of barley, oat, rye and wheat resp. × 174.

examined, (figure 5), it will be seen at once that the appearance offered by the transverse section gives a totally inadequate conception of the shapes of the constituent cells, many important details not appearing at all, especially in such small objects as the grass stem, the total thickness of which is 0.5 mm. or less in thickness. However, by means of maceration (in chromic acid for example) the cells may be set free from each other and thus examined. With the additional help of this method we may examine each tissue in turn beginning with the epidermis.

THE EPIDERMIS Figures 6-13).

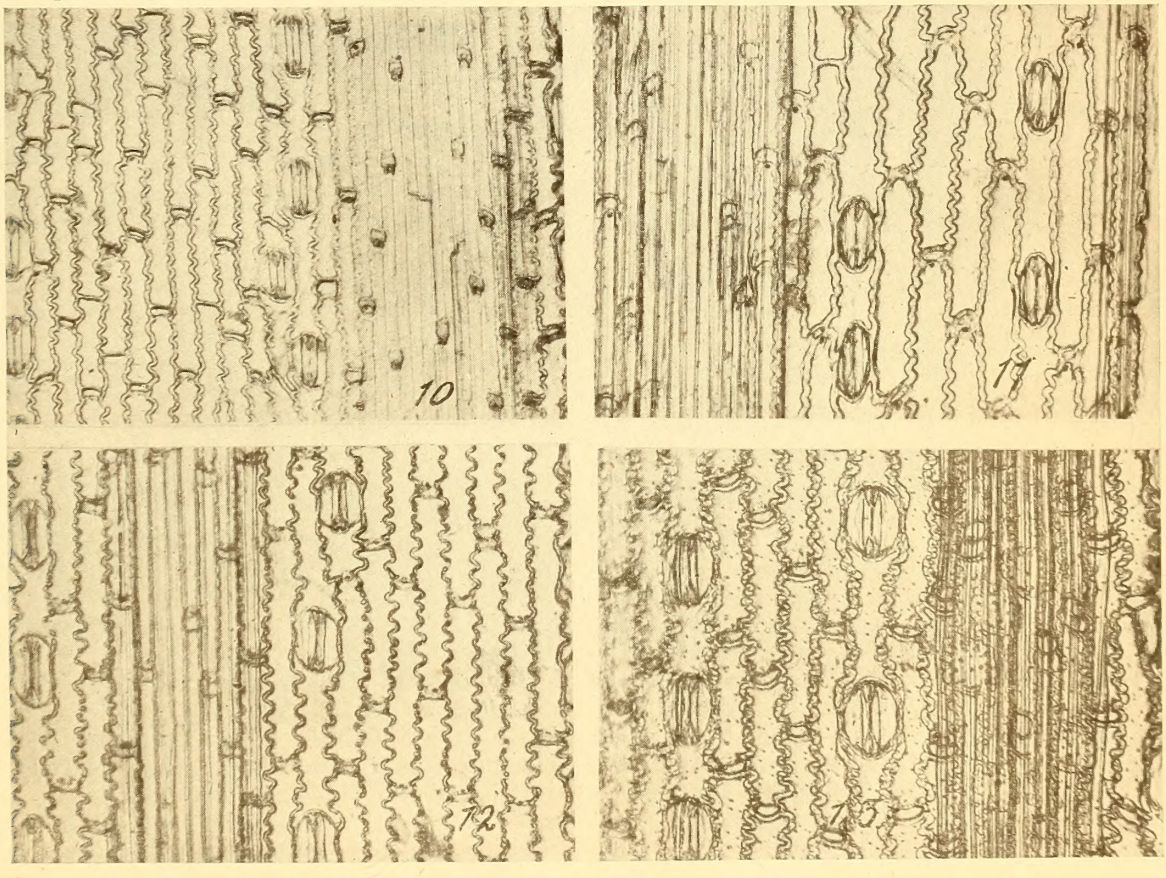
Examined *en face* the epidermis is seen, in general, to be composed of longitudinal zones of more or less elongated cells with undulating walls overlying the green tissues beneath, alternating with narrower zones of similar but longer cells with straight walls, and with narrower lumina.

The long cells are interrupted frequently by the so-called "dwarf-cells", which occur usually in pairs placed longitudinally, but may be either single, in threes or in fours. Of the pair, one cell is thin-walled and stains readily in the manner of the epidermal cells in general. This, when there is but one dwarf-cell in a position, is the cell which may assume the form of a trichome usually shaped like a cat's claw. The other is thicker walled, usually, and the walls are strongly silicified. Wiesner (1900) states that this is the case and Hoehnel (through Haberlandt, 1909, p. 105) represents them as single. Only one of the pair however, presents this character. The representation by Hoehnel seems to be referable to the circumstance that sometimes the cells in question are very small and sheared upon each other so that they can be resolved microscopically only in depth and not transversely (figure 14). In barley especially they are very small and difficult to resolve. In wheat however the silicified cell may be quite large relatively.

The long cells of the epidermis are interrupted also by groups of four cells forming the stomata. These are organs which are capable of forming openings through which gasses can pass into and out of the stem (figures 29a-d; 15). The four constituent cells are arranged in the grasses in a transverse row. The two adjacent ones, the "guard cells", are slender, and have a slit between them which opens and closes in life according to physiological conditions. The outer two cells are the accessory cells. The relations are best understood by examining a transverse section (figure 15).

Epidermis of the stem. The epidermis of the stem and of the leaf both present similar fundamental features as just described. They are, however, sufficiently different in details as to demand separate examination. (figures 6-9).

It is practically impossible to fit a single description to the epidermis of the stem for the reason that it shows marked differences in different portions of the internode. In the lower portion, the cell walls (in wheat, e.g.) are quite straight and thin, the dwarf cells are longer and very simple in structure. The stomata are few in number and less differentiated. In the upper portion, on the other hand, especially where the internode is not covered by the leaf-sheath, the cells have walls which are thick and undulating, and they occur in longitudinal zones alternating with zones of cells with straight walls. The dwarf cells are here strongly



Figures 10-13. — The epidermis viewed en face of the lower (outer) surface of the leaf sheath of barley, oat, rye and wheat resp. × 170.

compressed longitudinally (figure 14), and the stomata well developed. Indeed so much difference is there that it is difficult to recognize that one is dealing with the same stem. It will be readily understood that it becomes much more difficult to distinguish between different kinds of straws if only the epidermis from the lower portions of the internodes is regarded. Such characters as may enable one to make these and similar distinctions are found only in the upper part of the internodes.

Epidermis of the leaf (figures 10-13). In straw, in the ordinary commercial sense, the leaf blades are present in such small quantities as to be negligible. They are broken off in threshing and become as chaff. The leaf sheaths however are practically always adherent and form part and parcel of the straw and constitute a

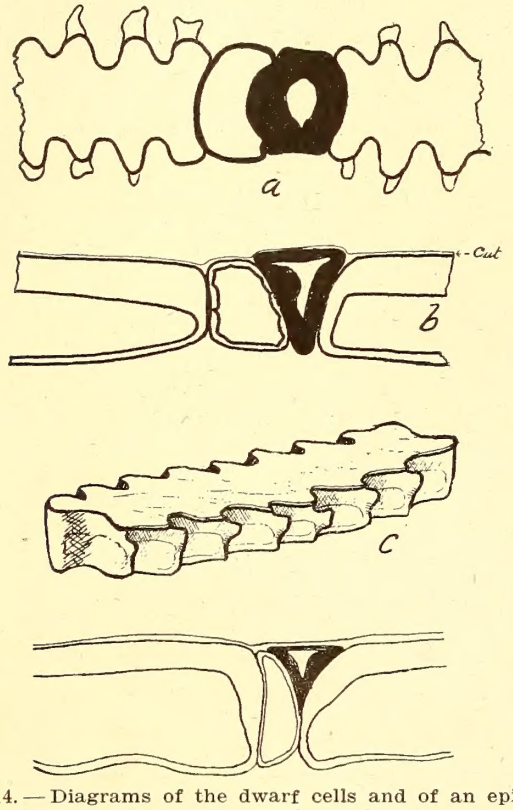


Fig. 14. — Diagrams of the dwarf cells and of an epidermal cell (wheat). **a**, dwarf cells, **en face**; **b**, lateral view; **cut**, cuticle; **c**, epidermal cell in perspective; **d**, dwarf cells of barley.

not inconsiderable proportion of straw paper pulp. The epidermis is moreover more evenly and fully developed throughout the whole length of the leaf-sheath. The longitudinal walls of the longer cells of the outer surface are thicker and usually strongly undulating, the dwarf cells may be developed into short protruding hair (wheat) and are generally in twos (figures 9 and 13). The epidermis of the thin leaf margins and of the inner surface of the leaf-sheath is very thin, as are the walls of the cells. They are here also without undulations, and dwarf cells are relatively few. The relative amount of epidermis from the leaf-sheath as compared with that of the stem, together with its uniform character makes it an important means for the identification of the kind of straw, especially in the form of pulp.

THE INTERNAL TISSUES.

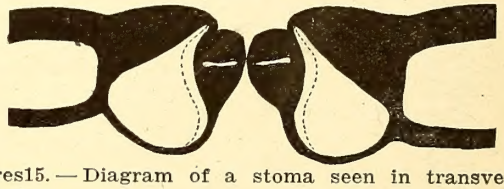
The epidermis encloses a variety of tissues and a still greater variety of their component cells. The latter may be segregated into two groups, according to their dimensions; roughly, those which are rather short **(parenchyma)** and those which are elongated **(prosenchyma)**. These distinctions are made chiefly for the purposes of description, and are used as such. It has been pointed out that the epidermis is differentiated into longitudinal zones ("fluting") which are readily distinguishable by the character of the cells composing them, and most easily by the presence or absence of stomata (figures 6-13). Those with stomata may be called the stomatal-zones for convenience. These distinctions hold for both leaf and stem and with them in mind we may proceed to consider the arrangement of the internal tissues of both.

Internal Tissues of the Stem.

The Chlorenchyma.—Lying just beneath the pore zones of the epidermis are to be found corresponding zones of very thin walled and loosely arranged cells which during the life of the plant contain green coloring matter (chlorophyll) (figure 4, ch.). These cells constitute the chlorenchyma which appears merely as green color to the eye, arranged in longitudinal zones. The chlorenchyma is the active seat of starch formation, for which purpose carbon dioxide is necessary. This finds its way by diffusion into the chlorenchyma through the stomata pores. This relation explains the distribution of these pores in longitudinal zones.

The chlorenchyma is best developed in the exposed upper part of the internodes, especially of the topmost slender internode which bears the grain (figure 4). As one descends an internode, the chlorenchyma becomes less and less conspicuous, until near the base it may not be present at all (figures 2 and 3). It has been noted above that there are here very few stomata, corresponding with the absence of chlorenchyma.

The "fluting" can sometimes be seen e.g. in wheat, by the naked eye to occur roughly in pairs. This is



Figures15. — Diagram of a stoma seen in transverse section, barley.

brought out clearly in a transverse section (figure 4). in which it is seen that the chlorenchyma strips are paired with reference to certain groups of cells (vascular bundles). Sometimes the neighboring strips of adjacent pairs run together, making a group of three; in other instances the spaces between the pairs are equal to the spaces between the members of a pair, so that the fluting is less obviously regular, but more so in some straws e.g., wheat, than in others.

The chlorenchyma in the lower internodes is more tangentially compressed than in the uppermost, is relatively shallower and is more irregularly disposed. The topography as revealed in transverse sections is fairly characteristic for each of the grains (figures 16-19).

The Zone of Fibres (bast).—The longitudinal zones of epidermis devoid of stomatal pores are on the other hand underlain by a mechanical tissue composed of much elongated cells (fibres). To each zone, and lying just below the fibres, is a vascular bundle (figure 4). According to the age of the stem and to the vertical position, the extent of fibrous tissue varies, it being relatively greatest in the lowermost part of the internode, and bears an inverse relation to the chlorenchyma

zones. Here the fibrous tissue underlies the chlorenchyma zones, thus forming a continuous layer of mechanical tissue around the whole stem, having an average depth of about 0.5mm (50 microns) (figures 3, age depth of about 0.5 mm. (500 microns) (figure 3,

Embedded in this layer is a tangential series of vascular bundles, one underlying each surface ridge and therefore between adjacent flutings. This is the zone of fibres, and it is the material which is chiefly important in paper making, although the other elements occur more or less according to the grade of paper.

The Pith (Fundamental Tissue).

We use this term to embrace all the remaining tissue lying within the zone of fibres, excluding the vascular bundles. The constituent cells are parenchyma about two to four times as long as broad (pa., figure 5), and relatively thin walled. The walls are for the most part however, quite rigid in the dry straw, and they contribute no small share to its mechanical qualities in this condition. Only at the innermost limits of the pith they are soft walled and lax. The condition is due to the dying off of the innermost pith cells as the cavity of the straw is formed during the development of the plant. The condition is well illustrated by the oat (figure 17).

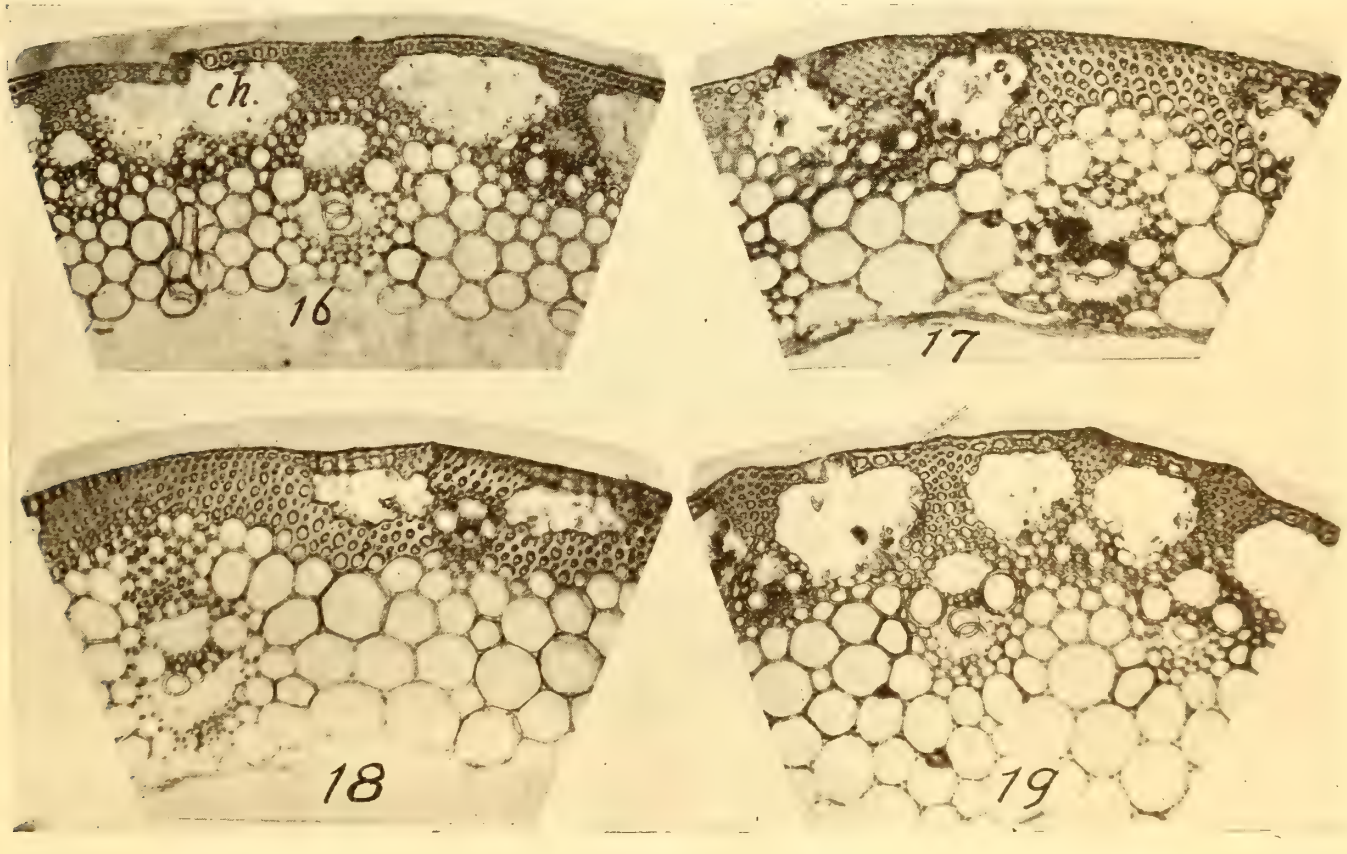
Fibro-vascular Bundles.

Lying in the pith is a series of vascular bundles of large size.[6] These bundles are of rather complex structure (figure 24), and have for their function the transportation of water and food materials up and down the stem and leaf of the plant. The portion which has to do chiefly with the movements of water is the xylem or wood (vessels) and can be recognized in the accompanying figure as four large openings disposed like the eyes, nose and mouth of the face, and surrounded by cells of much smaller caliber. The small thick walled cells between the eyes are also wood vessels. Most of the wood vessels can be recognized in pulp or macerated material by the numerous slit-like pits in the walls.

The wood-cells are primary and secondary—those first formed during the development of the stem, and those later formed. The first formed have very thin walls strengthened by rings or spirals (figure 5, **x**). With the elongation of the stem during growth the thin walls are ruptured, and the rings are in consequence spread apart longitudinally, as are also the turns of the spirals. In pulp, rings and spirals may both be seen. The secondary wood cells are thick walled, but penetrated by pits which are more or less oval or slit-like in form and regularly disposed in longitudinal series, suggesting the rungs of a ladder (figure 5). The ends of the wood cells are transverse or more or less oblique —at an angle of scarcely more than 45 degrees and are usually open, so that a series of cells make a continuous tube. Between the wood-cells with pitted walls and those which have only ring thickenings, there are various intermediate stages. On the two sides of the primary wood there are some very thin walled elongated wood cells with transverse or slightly oblique walls. These elements are of very delicate structure, and disappear readily under chemical treatment in making pulp.

Wood cells form but a very insignificant part of pulp, due to their originally small proportion and to the breaking up of the primary cells into the minute frag-

[6] There is strictly speaking more than one series, but for the purpose of this description it is unnecessary to distinguish between them.



Figures 16-19. — Sectors of transverse section of the terminal internode of barley, oat, rye and wheat, resp. x 146. — Ch., chlorophyll tissue space, the tissue disintegrated in these sections.

ments in the shape of the aforesaid rings and spirals. The large wood cells (vessels) are about 40 microns in diameter (micron = 0.001 millimeter), while the small ones are about 7 to 8 microns, or thereabout, in diameter, roughly about one-fifth the diameter of the large vessels.

Placed radially and on the outside of the wood, forming as it were the forehead of the fase, is a small group of very thin walled cells with very narrow lumina (ph. figure 24). This is the phloem, concerned chiefly in the movement of food materials. The cells are of two kinds, sieve tubes, which have thickened end walls and more slender cells lying alongside them, the comparison cells. Like the wood cells, they are elongated elements, very slender and delicate, and usually disappear during pulping, and contribute not at all to the final product.

Surrounding the wood and phloem is a narrow layer of fibres (f, figure 24), or rather fiber-like cells, with pitted walls and somewhat oblique (about 45 degrees) or transverse end walls. The fibers on the outside of the phloem (between it and the epidermis) are numerous enough to form a small bundle. This is the case also on the inside of the xylem (toward the center of the stem). The lateral walls when seen longitudinally are irregular when they impinge on the surounding parenchyma. While contributing to the "fibers" of pulp, they constitute only a small proportion of shorter elements.

Internal Structure of the Leaf Sheath.

The leaf is composed of elements which are quite similar to those above described for the stem, but arranged somewhat differently, due to the fact that the leaf is a flattened organ, the upper surface (which lies against the stem) being smooth, and the lower ribbed. In a transverse section (figure 25) it is seen to be segmented into similar areas of loose parenchyma which behaves quite as does the pith in the stem, breaking down early to leave cavities. Each partition is composed of a vascular bundle, having bundle of fibers (mechanical tissue) between it and the lower (outer) epidermis, and a group or bundle of larger, much elongated and fiber-like cells between it and the upper (inner) epidermis. The parenchyma which fills the ribs just below the lower (outer) epidermis is composed of smaller, chlorophyll bearing cells, through which a small bundle and a group of fibers run, parallel to the larger bundles just noticed. The amount of fibrous material is not inconsiderable, forming approximately one-fourth to one-third of the total amount of fiber of an equal length of stem. A peculiar anatomical feature of the leaf-sheath is the occurrence of very long, thin walled tubular cells, (l, figure 25), forming a small group of fibers between the large bundles and the upper (inner) epidermis. They can hardly be classed as fibers—or at any rate they cannot be compared with fibers in point of strength, since the walls are thin and the lumen large, measuring 60 microns, more or less. The end walls are transverse, slightly oblique, or forked. They are relatively few in number, but can usually be found in pulp or straw paper.

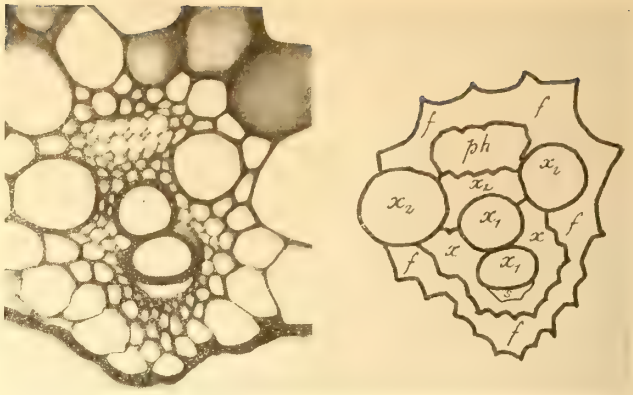


Figure 24. — Transverse section of a single bundle from the stem of wheat. x 232. **f.**, fibers; **ph.**, phloem; **s.**, cavity formed by splitting of the tissues away from the primary wood trachea; x_1., primary wood vessels (tracheae); x_2., secondary wood vessels.

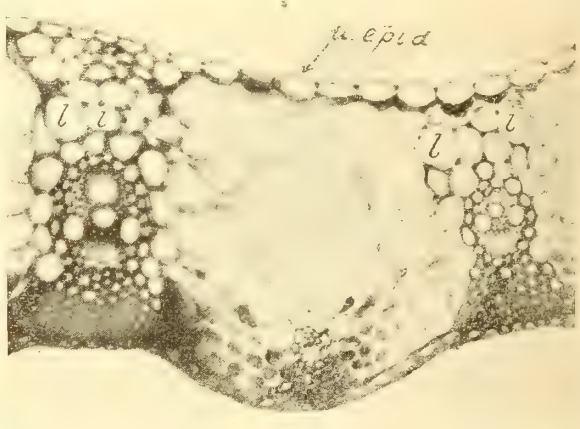
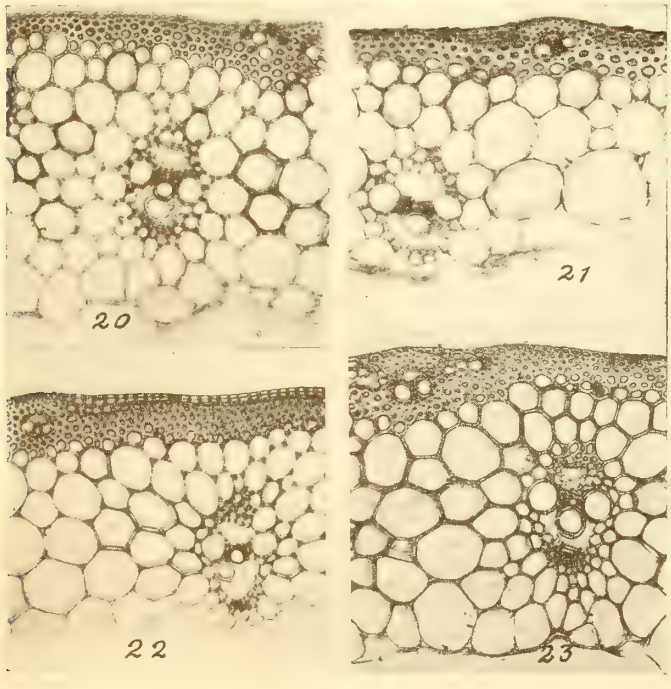


Figure 25. — Portion of a transverse section of the leaf sheath of wheat. Note the wide (l, l) thin walled cells just above the bundles. **u. epid.**, upper (inner) epidermis. x 130.



Figures 20-23. — ectors of transverse sections of the middle region of the lower internode of barley, oat, rye and wheat, resp. x 97.

False Nodes.—The above described structure fails almost entirely at the base of the leaf-sheath, where the motile organ or false node occurs. There is an entire absence of specialized chlorenchyma, and the parenchyma is thick walled. The walls, however, in common with those of the bundles of fibers, which form a

very conspicuous feature in a transverse section (figure 26) are soft and yielding during the growing period. The bundles in question accompany the fibro-vascular bundles, and the component cells are fiber-like, with highly elastic walls, seen as darker groups of cells in figure 26.

Chemical Characters of the Tissues.

When the cell-walls are first formed, they are composed of cellulose, with a layer (the primary membrane) of pectose between the adjacent walls. As development proceeds, additional substances (lignin-bodies) the chief of which passes under the term lignin are added to the walls.

Stem.—In the mature straw, all the cell-walls become strongly lignified with the exception only of the phloem, the thin-walled xylem (wood) lying on either side of the primary wood, the collapsed pith cells, and the chlorenchyma. The lignified tissues therefore are the epidermis,[7] all the fibers, all the wood vessels, (tracheids) and the parenchyma (save the inner pith cells and chlorenchyma) (figure 4). On account of the completeness of lignification the cellulose of straws (grain straws) is regarded chemically as lignocellulose.

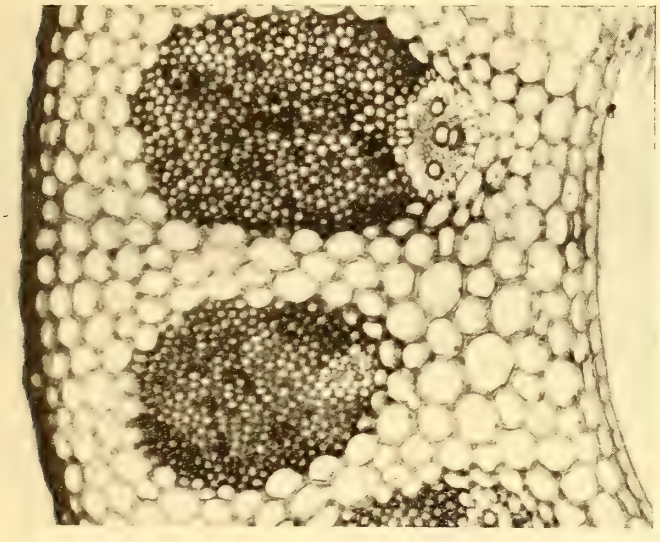


Figure 26. — Sector of a transverse section of a false node (leaf base) of wheat. x 105.

Leaf Sheath.—In the basal region the fibers between the bundles and the lower epidermis are wholly lignified. Of the long cells (1,1, figure 25) some, ut not all, are lignified, those namely which lie near the middle vertical plane of the bundle. The true fibers occur, as they do next the upper epidermis in the left hand (the larger) bundle in figures 25, these are lignified. The lower (outer) epidermis is weakly lignified only, the inner not at all. The fiber and xylem (except the soft xylem) are also lignified. The parenchyma is not.

In the upper part of the leaf sheath only the fibers between the bundles and the outer epidermis are lignified, as also the fibers and xylem vessels of the bundles. The thin papery leaf margin is unlignified for some distance from the edge, probably as a result of early desiccation.

In the false node there is no lignification at all, excepting only the xylem (wood) vessels.

The epidermis is clothed by a very delicate membrane which extends over the whole surface of the plant, the **cuticle.** This membrane is impregnated with a wax-like substance which renders it very hard and resistant, and gives it a highly glossy finish characteristic of straw. It repels even hot water after considerable boiling. There is some evidence also that the inner cells of the parenchyma and the associated cells are more or less impregnated with wax-like materials, since their primary walls are very resistant to concentrated sulphuric acid even after twenty-four hours treatment. This may be due simply to a high degree of lignification however.

There is furthermore a considerable degree of silicification of both cuticle and more of less of the tissue beneath. The presence of silica gives to the straw a corresponding degree of hardness and smooth finish. The amount of silica is sufficient in many cases to preserve the form of the cells even after the complete extraction of the cellulose and other materials by suitable reagents. An analysis of four samples of straw for silica gave the following percentages of the total dry matter.

Barley	2.07	Rye	2.18
	1.78		2.14
Oats	3.46	Wheat	2.30
	3.46		2.44

It is the amount of silica in the superficial tissues which renders the surface so very hard and resistant. It is well known that the same result is seen in the surface tissues especially of bamboo, rattan, and the like.[8]

Zacaton (Elicampes macroura) according to Brand and Murrill (1915) contains silica to the amount of 6.5 to 7.5 on the total straw. This is "very high."

In the preparation of paper pulp the pectose is altered, setting the cells free from each other, and the cells are more or less delignified. The delignification is carried on much further in bleached pulp than in the unbleached pulps. Papers subjected in manufacture to a 20 per cent and to a 15 per cent lime cook, and a "Kraft" paper all showed pronounced lignin reactions with the Klason and with the Cross and Bevan methods, while bleached papers from wheat straw subjected to a 6 and a 10 hour soda cook, and from oat, gave only very slight lignin reactions. An unbleached oat gave a distinctly stronger lignin reaction.

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[7] The lignin reaction proceeds very slowly in the outermost fibers and in the epidermal cells. This seems to be due to other substances possibly of the same nature as that which renders the cuticle waxy. A light yellow color is noticeable in these tissues.

[8] The following figures are afforded by C. Wehmer (1911):

	Total ash	of which silica constitutes
Barley	5-7 %	50-60 parts
Oat	—	50-66 "
Rye	5-10	60-70 "
Wheat	3-5	50-60 "

These figures are much higher than the previous given, but of course no adequate comparison may be instituted without due regard to place effect and other possible conditions.

COMPARISON OF THE VARIOUS STRAWS BASED UPON STRUCTURAL DIFFERENCES.

External Gross Character.

The four straws under examination may, if entire, be readily distinguished by their stature, thickness, and the shapes of the individual internodes and the minor but nevertheless diagnostic characters offered by the false nodes, by the shape of the upper part of the internode just below the nodes, the sub-nodal constrictions, and claws. The keys given below, as being the briefest methods of description and at the same time most easily usable, present the contrast of structure in summary form. It will be understood that such keys are useful only as descriptive of the four straws included, and would require modification and extension if other straws had to be considered (*). A possible qualification might be forced even by races within the species, and even by the age of the individual. Thus Carrier e.g. bases his classification of grain seedlings on the presence or absence of claws, finding them present

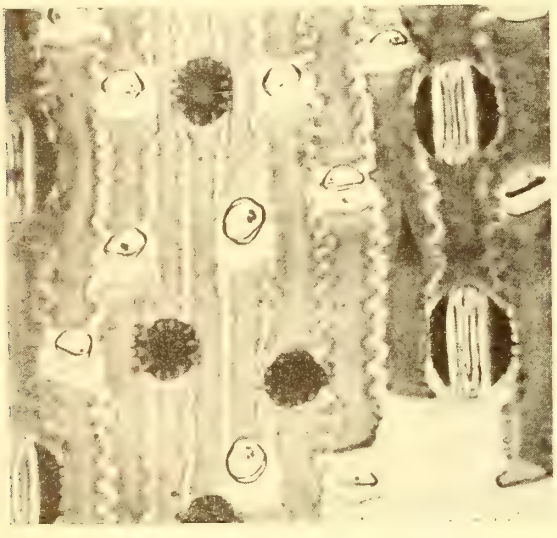

Figure 27. — Epidermis of wheat to show the crown cells. The dwarf cells are also in evidence by the black outlines, due to included air. The cells are somewhat separated from each other by maceration. x 310.

in all the grains but oat. It was difficult to find evidence of claws in the sample of wheat straw supplied for this work, but other samples showed them to be present, but quite irregularly. Thus they may be present on one side only, or totally absent, or, when present, they may show much difference in size on the two sides of the leaf. Rye, in common with wheat, betrays a considerable amount of variation in this respect.

The characters used in the keys are for the most part such as may be detected readily even if the straw is broken, and when the fragments are small. When pulped however, identification must rest upon minute anatomical characters which offer greater difficulties of choice and application. Such characters are the length of fibers, sizes of stomata, the presence or absence of trichomes ("comma cells," Weisner, 1865,) characters of epidermal walls, and the like.

Identification Keys Based Upon External Characters.

Interior face of leaf sheath smooth; ligule long (*ca.* 4 mm.); claws absent; false nodes usually much shorter than broad; terminal internode 2 or more mm. in diameter near tip—oat. Interior face of leaf sheath rough, more or less, with upwardly directed short, stiff trichomes (comma cells); ligules short (1 mm.) Upper part of terminal internode pubescent or hirsute, the internode tapering to slender dimensions (1 mm. diameter)—rye. Upper part of terminal internode smooth thick toward apex. Claws prominent, always present —barley. Claws sometimes absent, small or various in size—wheat.

The dimensions of the false nodes when wet and dry afford a means of identification of some value, though more difficult of application. The following tables are examples of such measurements.

Measurements (diameter and length) of false nodes of barley, oat, rye and wheat in swollen condition, in millimeters.

	Basal		Middle		Top	
	Diam.	Length	Diam.	Length	Diam.	Length
Barley	5	3.5	4.8	4	4.2	5.4
	4.6	4	4.5	5.3	3.7	7
Oats	5.5	2.5	5.5	2.6	5.3	3.2
	4.6	2	4.5	2.7	4	2.6
			5.4	2.8	5	3.5
Rye	4.5	3	4.4	4	3.5	5.2
	4.5	2.5	4.4	4	3.6	4.5
	5.2	3.8	5	4.7	4	4.5
Wheat			4	2	4	4
			4.5	3.5	4.5	3.8

Measurements (diameter and length) of false nodes of barley, oat, rye and wheat, to the nearest half-millimeter, when dry.

	3rd.		2nd.		Top	
	Diam.	Length	Diam.	Length	Diam.	Length
Barley	2.5	3	2.5	4	2	4.5
	2.5	2.5	2.5	3.5	2	4
			3.0	3.5	2.5	4.5
	2.0	2.5	2	3.5	2	4
			2	3.5	2	4.5
Oats			4	1.5	3	2
			4	2	3.5	2
			4	2	3.5	2
			4	2	3	2
			3.5	2	3	3.5
Rye	3	3.5	3	4	2	4
	3.5	2.5	3.5	3	2.5	3.5
	3	2	2.5	3	2	3.5
	4	3.5	3.5	4	3	4
	3.5	3	3	3.5	2.5	4
Wheat			3.5	3	3	3
			3.5	2.5	2.5	3.5
			3	2.5	2.5	3.5
			3	2.5	2	3
			3	3	2.5	3.5

COMPARATIVE ANATOMICAL CHARACTERS OF STRAWS.

Comparison of Distribution and Characters of Tissues as Seen in Sections.

1. Transverse section of the terminal internode (figures 16-19). There is little that can be regarded as sufficiently characteristic in the structure as seen in transverse section to serve as diagnostic. Of two rather obvious points, that of size has already been

(*) See the bulletin by Lyman Carrier, 1917.

made use of in one of the preceeding keys. It may be added here that the thickness of the wall of the terminal internode near the tip is equally characteristic, and is for the different straws as follows:—

	Thickness of wall	Diameter of straw
Barley	1	6
Oat	1	8
Rye	1	3—4
Wheat	1	4

On this point therefore, rye and wheat may be distinguished from oat and barley.

The second point is found in the number of chlorenchyma spaces which may be counted in the total transverse section. Rye has by far the fewest, namely, about 18 to 20, while the other species have from 30 to 36, barley having 32, wheat 34 to 36, and oat 36 to 38. These numbers are approximately twice the numbers of bundles in the innermost series. The fact that the chlorenchyma spaces may be double instead of in pairs separated by a small bundle may make it necessary to regard a single one as two, or to rely rather on a count of the large bundles which lie free in the parenchyma. Thus, the stem in figure 3 has 37 undles, which is, however, not a terminal internode.

A third feature is the character of the lining of the fistula formed y the dead parenchyma. It is thickest and pavement-like in the oat (figure 17), well defined in all but the wheat, in which it is loose and ill-defined in texture, not forming a smooth lining.

Summarizing these characters in the form of a key we have the following:—

A. Thickness of wall of fistula (terminal internode, near its apex) one-fourth to one-third the total diameter
  a) Collapsed pith cells forming a clear cut pavement; or
  b) Number of bundles in innermost series about 12 . . . . . rye
  aa) Collapsed pith cells loose, not forming a pavement; or
  bb) Number of bundles in innermost series about 18 . . . . . wheat

B. Thickness of wall of fistula one-sixth to one-eighth that of total diameter.
  (a) Pavement formed by pith-cells thick; or
  (b) Parenchyma cells large . . . . . oat
  (aa) Pavement formed by pit-cells thin; or
  (bb) Parenchyma cells one-half the diameter of those in oat . . . . . barley.

The amount and disposition of the fibers (mechanical tissue, bast) is correlated with the chlorenchyma, there being relatively more fibers toward the base of the (top) internode, and relatively fewer toward the apex. In relation, however, to the area of the transverse section the fibrous tissue is greater toward the apex, this being apparently correlated with the mechanical conditions associated with the reduced diameter. Concerning the character of the fibers we shall speak beyond.

2. Transverse section of basal internode. If anything, the lower internodes offer less to seize upon for purposes of identification than the terminal. Bearing in mind the difference of structure as between the upper and nether parts of the internode, the middle portion has been taken as a standard of comparison. Of the four straws, the oat stands out clearly on account of the small number of parenchyma cells, and of their large size. As in the terminal internodes, the collapsed pith cells make a thick pavement lining the fistula. In the oat also there are only about 20 large bundles free from the fibre layer, while in the others the number is greater, from 24 (wheat, rye) to 28 (barley).

Comparison of the individual tissues and of their elements. Epidermis (figures 6-13). Of all the tissue systems, the epidermis lends itself most readily to identi-

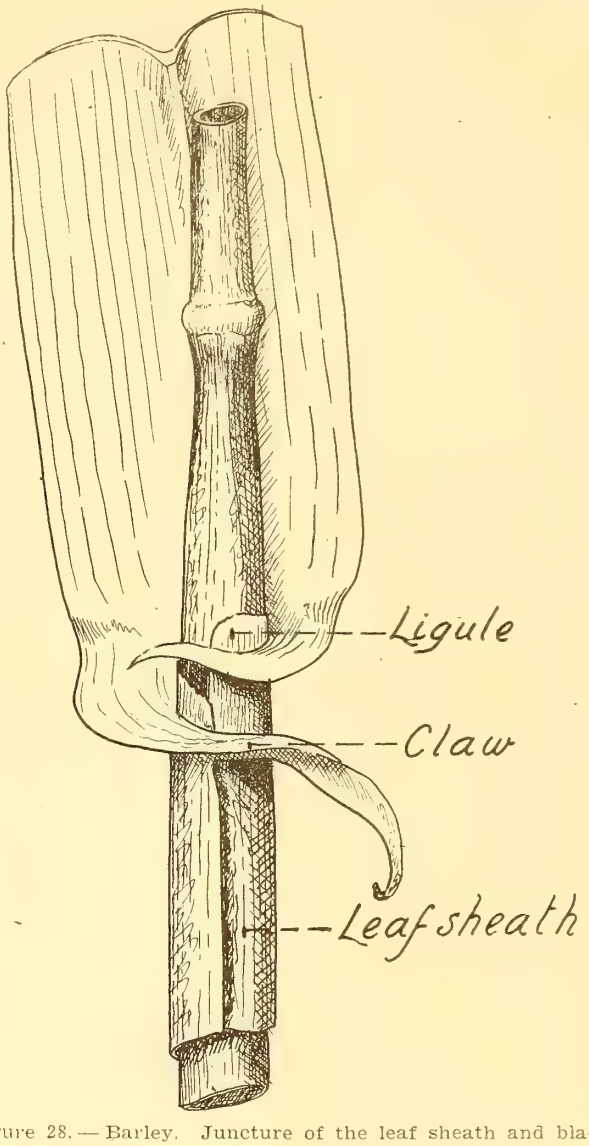

Figure 28.—Barley. Juncture of the leaf sheath and blade to show the claws and ligule.

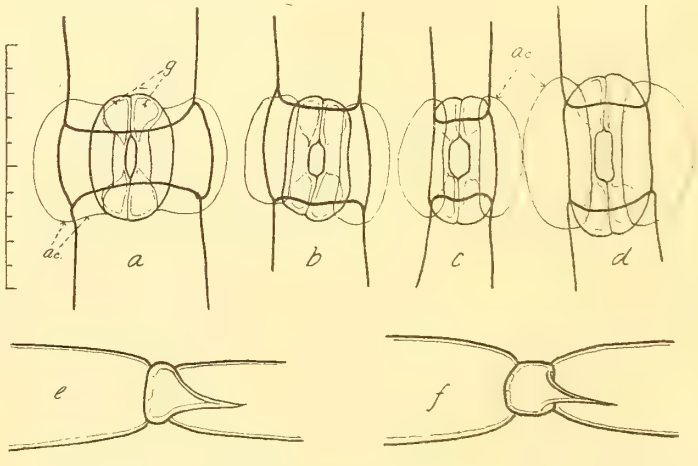

Figure 29.—Stomata and trichomes inner (upper) epidermis of the leaf sheath of (a) barley (b) oat, (c) rye and (d) wheat; also the trichomes of (e) rye and (f) wheat; **g.**, guard cells; **ac.**, outline of accessory cells. Drawn to the accompanying scale

fication, since it is more distinctive of the genus.

Wiesner's (1900) findings are of interest at this point. He says that the bast cells of the four cereal straws (here under consideration) are so similar as to afford no characters for certain differentiation, while the size and form of the epidermal cells are quite distinctive. Those in rye, wheat and oat he continues, have a pretty regular rectangular general outline. Those of rye have strongly sinuous limiting outline, while those of wheat are straight. Oat on the other hand has epidermal cells with a gently wavy outline. Those of barley are rhomboidal or trapezoidal in contour. The writer in view of the facts below presented feels that Wiesner's description is quite inadequate.

Fragments of the epidermis, or at least individual cells are easily found in paper pulp, and since they of all the elements show the least amount of distortion, their characters can be seized upon with corresponding readiness and certainty. Of the individual elements (cells) it is difficult or impossible to find those of stomata and of dwarf cells in bleached papers, since in these the treatment completely dissociates the cells in question, while their small size allows them to be washed away. In unbleached papers, on the other hand, fragments of epidermis sufficiently big to carry all the kinds of cells composing it can be found, thus permitting identification.

The epidermis of the outer surface of the leaf-sheath differs from that of the stem in certain details, and, inasmuch as for constant length of straw there will be more leaf epidermis present in pulp, it is quite as important an element to be considered as the stem epidermis, if not more so. The leaf blades are in minor quantity and are almost negligible in this respect.

As has already been said above, the epidermis is not uniform in structure, but consists of alternate longitudinal zones; those roofing over the chlorenchyma spaces, and recognizable by the stomata (stomatal zones), and those underlaid by fibrous tissues, devoid of stomata (non-porous zones). The latter, except in wheat, do not afford readily differentiable characters. The component cells are straight-walled (except in the leaf of wheat) and narrow, roughly about one-half the transverse diameter of the cells of the stomatal zones. These alternate, in a longitudinal sense, with the minute dwarf cells, which are either single, or in pairs. In the former case the dwarf cell is from the point of view of morphology a trichome of small size. When two are present, the upper (distal) one is a trichome. In the wheat in addition to the dwarf cells, there is a peculiar cell, roughly circular (*ca* 30 microns in diameter) in outline *en face,* and round or quadrangular in the stem, which, on account of the large amount of unmodified cellulose present, take up stains (magenta, Bismarck Brown, safranin, etc.) more readily than the remaining epidermal cells, excepting only the accessory cells of the stomata. By their consequent darker staining reactions, they are more readily seen in suitably stained preparations, as seen in figures 9 and 13, and especially in figure 27. In the leaf they assume the form of trichomes.

On account of their shape I call these cells *'crown' cells.* Since they are absent from the other grains which we are considering, the presence of crown cells definitely identifies wheat.

In barley wheat and rye, trichomes are present. They are especially developed on the terminal internode of rye, and, in fragments of epidermis, their bases are seen as large oval cells in the positions of dwarf cells. Smaller ones sometimes occur on the leaf sheath (outer surface) in wheat.

They are absent from the oat excepting only that they are present on the upper surface of the leaf-blade and its margins. Their form is such that the sharp claw-like end lies for the most part parallel with the leaf-surface and so the roughness produced is not marked. This permits their recognition with some certainty. In the epidermis of the stem and outer (lower or dorsal) surface of the leaf sheath, we note the following:

The cells (exclusive of stomata and dwarf cells) have much more strongly (1) wavy or sinuous longitudinal walls in the leaf-sheath. In the stem they are only slightly undulating, or, in oat, straight, or nearly so. Arranged in series based on waviness both in leaf-sheath and stem the four straws are as follows: Wheat=rye; barley; oat.

It is difficult to judge on this point as between wheat and rye, since the walls are thinner in the latter and so the waviness is masked. The waviness is most irregular in wheat and least so in oat, the four straws falling, as regards this feature, in the same order as the above.

The waviness and irregularity in the wheat are very characteristic, and enable one to identify it with considerable ease. The oat is equally distinctive by virtue of the relative or entire absence of undulations from the cell walls of the middle of the stomatal zones of the upper region of the leaf-sheath (3) the sinuosities increasing in amplitude toward the non-porous zones and toward the base of the sheath. When isolated, the straight walled cells are indistinguishable from the epidermal cells from the inner (upper) surface of the leaf-sheath and from the outer surface of the papery leaf margin, so that, unless leaf-fragments of sufficient size are available, positive evidence can be gained only from the sinuous cell-walls. The character of these sinuosities is well shown in figure 11, which however is from a part of the leaf sheath which does not show the straight cell walls, that is, approximately, the middle region.

Rye and barley can be distinguished readily enough from wheat or oat, but not easily as between themselves, if the character of the undulations is depended upon (figures 10-12). They are however easily separable by the absence or presence of trichomes at least as far as the lower part of the leaf-sheath is concerned and by the character of their walls, which are much thicker generally in the wheat.

The character of the undulations is more difficult to judge when the cells are isolated, since the lateral processes of the cell, corresponding to the undulations but lying below the surface, are much more pronounced. It is therefore necessary to obtain a microscopic image of the outline of the upper face of the outer cell wall, (see figure 14) that namely to which the cuticle is applied.

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(1) That is as to depth, but not as to the number of undulations per unit of length.

(3) Wiesner's description of the epidermal cells of oat has already been cited. It is evident that he had regard only to the epidermis of the stem. The waviness of the walls of the leaf-sheath epidermis is so evident, and it is so certain that the leaf-sheath contributes largely to the fiber in paper that it is quite necessary to have regard to the character of its epidermal cells.

An effort has been made to base distinctions upon the thickness of the epidermis cell walls, but this is difficult. The thickness varies with the level, the extreme thickness being found at the base (6 microns for oat), where the amount of fiber is also greatest, and the least thickness (2 microns for oat) just below the ligule. This character varies also with the maturity of the plant. In general however, the series seems to be the following, in order of thickness of cell wall.

Leaf sheath, near ligule: wheat =oat=barley; rye.
Near base: wheat; rye=barley; oat.

Wheat has the stiffest leaf sheath throughout its length, while rye and oat show the greatest change from base to apex. When all is said however, from the point of view here taken, this feature is of perhaps least value.

There are similar but not so great differences in the thickness of the cell walls of the epidermis in different parts of the internode, coupled with the absence, at the base, of stomata and stomatal zones. In all the straws, the thickness of the walls decreases toward the base, their sinuosities are entirely absent, and their caliber becomes much reduced. Indeed, the differences in the lower part of an internode are so slight as to be practically negligible, although, in unmacerated epidermis, the oat can be distinguished from the others by the thicker walls. The series are, in order of thickness of cell wall as follows:

Lower internode: near top: wheat (9 microns); oat (6 microns) = barley = rye.
Near base: oat (3-6 microns); wheat (2-3 microns = barley = rye.

The width of the epidermal cells of the stomatal zones affords an additional criterion of distinction which is of some help. The following measurements were made on five different leaves and five different stems, the leaf specimens taken near the ligule, and from the internode correspondingly near its apex. About 150 measurements of each species were made, each measurement being the total width of from five to twelve cells, taken transversely. Two sets of measurements were made several days apart, and they were found to check, this also in the case of the stomatal measurements just beyond.

Minimum, mean and maximum width of epidermal cells (with wavy outlines) of stomatal zones, (in microns):—

	Leaf sheath	Stem
Barley	16 - 20 - 25	15 - 17 - 18
Oat	25 - 27 - 31	19 - 21 - 23
Rye	22 - 24 - 28	18 - 20 - 22
Wheat	24 - 27 - 32	20 - 21.5 - 24

These measurements may not of course be taken as a single expression of unvarying size for each kind of straw, but they appear however to express with fair accuracy the relative values of the different kinds. The order of the series for both leaf and stem is therefor: Wheat; oat; rye; barley, there being less difference for the stem than the leaf. In the former the differences are too slight for practical purposes, and therefor can scarcely be used to advantage.

Measurements of length of the epidermal cells appear to be of less value that those of width. Wiesner (1900) gives the following dimensions determined by him.

	Length (microns)	Width (microns)
Barley	103-224	12-14
Oat	186-448	12-17
Rye	86-345	12-16 (14)
Wheat	152-449	18-24

(14) Hoehnel gives 36-90 as Wiesner's figures (from Wiesner 1867). In Wiesner 1900 they are given as 12-16, as above quoted.

Weisner does not tell us what epidermal cells they are that he measured, and it has become quite evident from my own observations that it is important to know this. That his data are of restricted value appears at once when they are compared with the following made by me on the epidermis which yielded my own measurements of cell width, given above.

Epidermis.— Length of cells in microns.

Species	Stem (lower internode) Upper part	Stem (lower internode) Lower part	Leaf-sheath
Barley	39-270	450	30-186
Oat	45-405	240	225-2100 (15)
Rye	30-270	630	45-300
Wheat	60-300	585	30-330

(15) The epidermal cells with straight (non-sinuous) walls are by far the longest, those having lengths of 1,000 to 1,500 microns being frequent.

The length of the cells varies very much with the position, the shortest occurring in the vertical series which include the stomata, the longest in the non-stomatal zones, where the outlines are either less wavy or not at all. In macerations, the latter might easily be overlooked. At all events, with such wide limits, and we note in passing especially the oat, the application of these measurements would have only an equivocal value.

The stomata show very considerable differences in size when the transverse and longitudinal measurements are taken separately. Measurements of 100 to 200 stomata taken from five specimens of upper part of leaf and of a lower internode gave the following data.

Measurements of stomata (in microns).

	Leaf sheath Length	Leaf sheath Width	Internode Length	Internode Width
Barley	50	26	47	26
Oat	**63**	25	55	29
Rye	56	29	58	31
Wheat	56	**37**	56	**34**

It has been seen that wheat has by far the widest stomata* while in the leaf sheath the oat has the longest. There is however considerable variation in the size of the stomata, especially from different regions of the organs which carry them. This offers a difficulty of course in view of the fact that in macerations the stomata from these regions are mixed together. The variation due to this alone is indicated in a general way by the following comparative measurements.

Stomata of internode.

	Basal internode (upper end) Length	Basal internode (upper end) Width	Terminal internode Length	Terminal internode Width
Barley	45	33	48	33
Oat	**60**	45	55	33
Rye	57	36	60	30
Wheat	55	**45**	55	33

Stomata of leaf sheath.

	New ligule Length	New ligule Width	Near base Length	Near base Width
Barley	43	24	51	19
Oat	60	27	49	30
Rye	54	24	62	31
Wheat	54	35	59	35

The discrepancies which are apparent in the above tables both for the stomata in similar regions and for different regions teach us that measurements must be used with caution and, beyond a very general purpose of distinguishing between one straw and all the rest, only when a sufficient number of measurements can be made, a caution which applies also to the other measurements given above.

Keys based upon the foregoing characters.

A. Epidermal cells with strongly undulating walls, at least toward the sides of the stomatal zones
.....leaf-sheath epidermis upper part.
Walls along the middle of stomatal zones thin and straight .....oat
Walls of nearly the same thickness and degree

(*) The width does not include the thickness of the wall of the two adjacent cells. The length is "over all" — that is. includes the total thickness of the end walls.

of sinuosity through the whole stomatal zone.

Sinuosities very irregular, stomata very broad (about 35 microns) crown cells present . . . . . .wheat

Sinuosities regular, crown cells absent.

Stomata with average width of about 50 microns . . . . . .barley

Stomata wider, average width of about 56 microns . . . . . .rye

B. Epidermal cells with straight, thick and only slightly undulating walls, or straight . . . . . .epidermis of internode

Crown cells present, stomata very wide (34 microns) . . . . . .wheat

Crown cells absent.

Wall straight . . . . . .oat

Walls slightly undulating.

Cells 15—18 microns wide, walls very slightly undulating, stomata small . . . . . .barley

Cells 18—22 microns wide, walls slightly undulating, stomata large . . . . . rye

It must be admitted to be difficult to apply the above criteria, but they seem to be the only ones available. It is more difficult to distinguish rye and barley, if one makes use only of the above marks, though easy to separate them from oat and wheat. The following paragraphs will however show that rye and barley are easily separable by other characters.

The preceding description of the epidermis does not include the epidermis of the inner face of the leaf sheath, that namely which lies in contact with the surface of the stem (internode). Although in most regards the structure is very uniform in all the straws there are certain differences which stand out prominently. In general, the walls of the long cells are very thin and straight, there being no suggestion of undulations, and they are very similar to each other in all the kinds of straw. The stomata and the dwarf cells however are distinctive.

The dwarf cells in wheat and rye are for the most part in the form of minute trichomes (figures 29 e-f). They are three or four times as numerous in rye than in wheat, and are so small that it requires either microscopic observation, or a sense of touch equal to that of the tip of the tongue to detect them. For this reason the latter method has been indicated in a previously given key. They are absent from the oat.

The stomata in rye and wheat (figure 29, c, d) are similar in that the guard cells taken together, are as broad as the long cells where they articulate with the guard cells, while in the oat and barley (figure 29, a, b) they are usually much narrower. In barley the fore-pore (the vestibule, or outer entrance) is small and well marked, while in oat it is not. Summarizing in the form of a key we have a

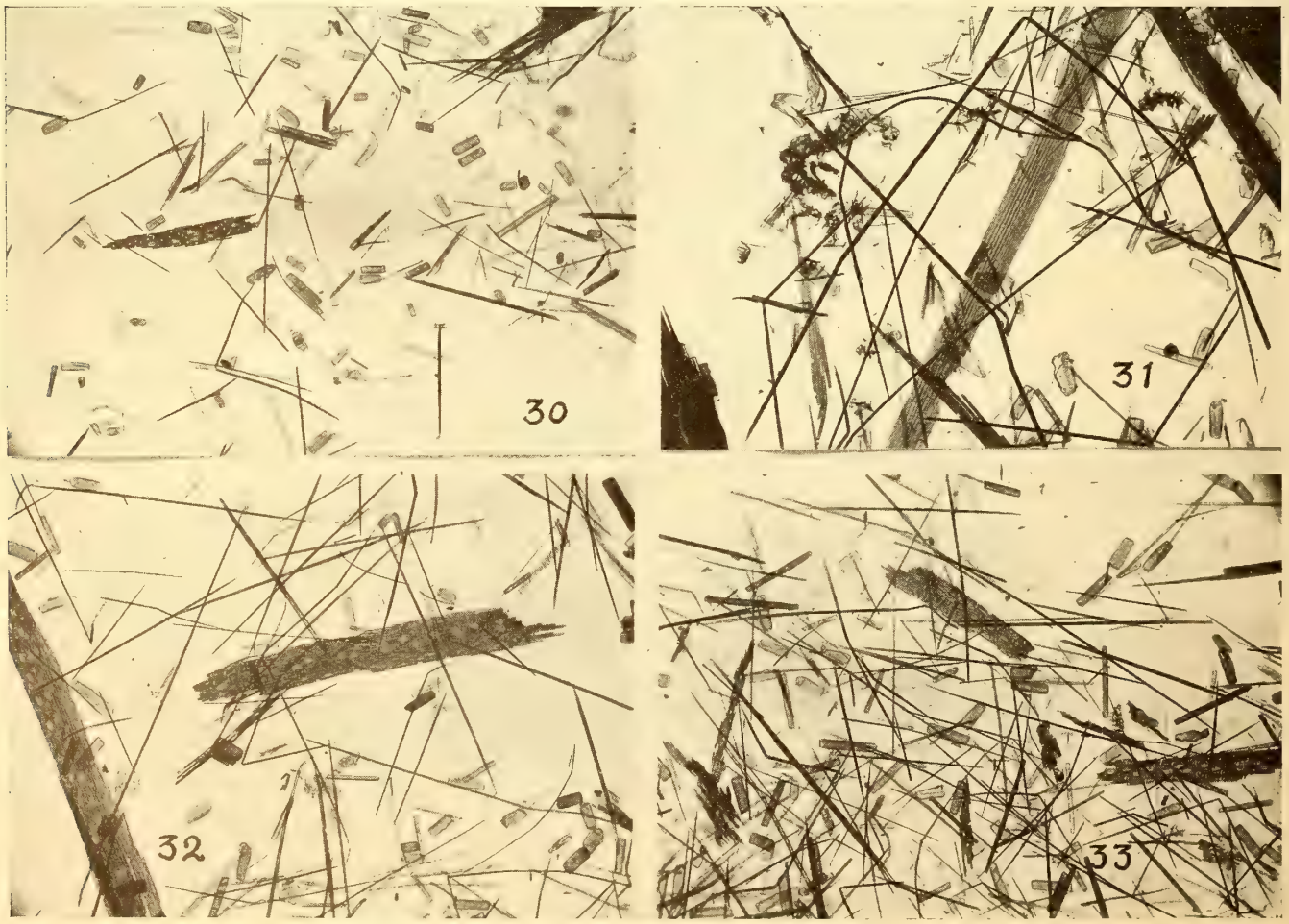
Key based on the characters of the inner epidermis of the leaf sheath.

A. Guard cells as wide as long cells. Minute trichomes present:

Stomata large (60—70 microns long) . . . .wheat

Stomata small (about 50 microns long). . . rye

B. Long cells wider than the guard cells; no trichomes in oat.



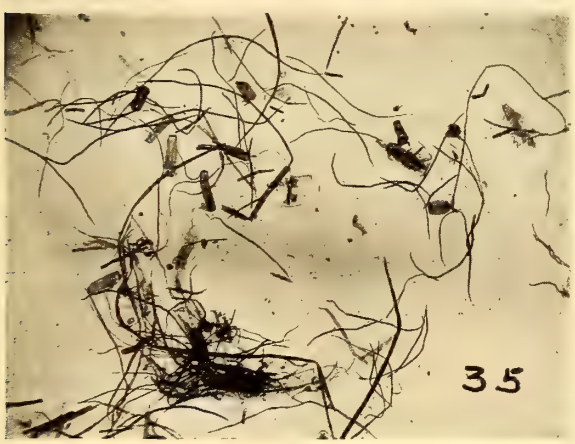
Figures 30-33. — Maceration products of barley, oat, rye and wheat resp. x 23.

Vestibule short and narrow, rectangular (figure 29a) .. .. barley

Vestibule nearly as long as the guard cells (figure 29b) .. .. oat

In studying the stomata in the inner epidermis of the leaf sheath, it is necessary to observe the precaution of excluding those along the thin, papery margin, as here they are narrow and hardly characteristic.

In evaluating these measurements, too much weight must not be attached to the averages. The short and slender fibers (6-10 microns in diameter) are reduced in number—at least they are not to be readily found—in bleached pulp, so that the character of the pulp is determined by the survival of the longer and the thicker (10-30 microns) fibers.



Figures 34-35. — Fibers and other maceration products from straw-pulp papers. Figure 34, oat; figure 35, wheat. x 20.

The mechanical tissues (fibers). Figure 30-33).

The mechanical tissues are made up of bast fibers composed of single cells with thick walls, and gradually tapering toward either end. The ends of the fibers are usually abruptly truncated by an oblique wall, or may be very blunt or even bifurcated.

There is little uniformity in length, as can be judged by inspecting the figures herewith (figures 30-33), and the thickness of the wall varies accordingly.

Table of fiber length (in millimeters).

	Number of counts	Stem max.	Stem min.	Stem ave.	Leaf sheath max.	Leaf sheath min.	Leaf sheath ave.
Barley	40	1.5	0.3	0.9	1.7	0.5	1.0
Oat	110-40	4.6	0.6	1.8	1.9	0.5	1.2
Rye	40	3.3	0.7	1.8	3.9	0.6	1.3
Wheat	5--20	2.4	0.7	1.6	1.7	0.5	1.2

In making the above measurements, certain long cells found in the leaf sheath were purposely avoided. These are the cells (some of which are marked 1, in figure 25), which occur along the ventral (upper) edge of the bundles and are especially long and thin walled, the walls with minute pores. Preparations were made so as to include these fibers only, excluding as far as possible the fibers from between the bundles and the lower epidermis. The lengths of the longer isolated cells (some are quite short) are:

Barley	about 1.7 mm.
Oat	5 to 8 mm.
Rye	about 4 mm.
Wheat	2 to 4.5 mm.

That is to say, these fibers, or rather fiber-like cells, are roughly twice as long as the true fibers in barley, and three times as long as in others, reaching the greatest length in the oat. They are rather readily found in paper pulp, forming but a small fraction of the whole.

An interesting and theoretically important question always comes up in regard to fiber length and its relation to position in the plant . Specifically stated, it is to be expected that the long internodes will have longer fibers than shorter ones? or will taller straw have longer fibers than shorter ones?

Rye is the tallest straw. The average length of fiber is little if at all greater than in wheat and oat. Measurements of fiber length for the terminal internode in rye, this internode being the longest, showed that the longest fibers were about 1.4mm long, whereas in the lowest basal internode they were 2.3mm long. There seems therefore to be no direct relation between length of straw and length of fiber.

It is of course very difficult to apply fiber measurements to pulped straw, since the working and the softening effect of the chemicals used result in bending and twisting of the fibers (figures 34 and 35). For critical determinations therefore, it is on the whole advisable to depend on the characters afforded by the epidermal cells.

These, together with wood vessels (tracheids) and parenchyma cells are always to be found in varying numbers, and more or less distorted, according to the length and character of the chemical treatment which may have been used. But of all the elements, the epidermal cells are the most resistant, and hold their original characters the best on account of their thick walls.

Xylem, phloem, and associated cells; parenchyma.

The impression is scarcely to be avoided that the structure of the straws of the various grains is remarkably uniform, a result to be expected from what we know of the general homogeneity of the group which they represent. This is especially true of the tissues which we have not examined in detail for differences, namely the tissues of the fibro-vascular bundles and parenchyma. Only the most general statements may be made with safety, and these do not lead very far. For example, we may say that in general the stature of the cells of all tissues is in barley (figure 30) less than in the other grains, and we have seen evidence of this in the measurements already given. Beyond this, only extreme minuteae, such as the shape and size of the pits in the wood (xylem), seem to offer any appreciable differences, and these are of very uncertain value. It would seem that, from the practical point of view, with the purpose in mind of seizing on differences which can be made use of for identification without too great difficulty, the features which have been presented above will meet the need.

The Chaff, (Glumes and palets.)

In the preceding account there has been no attempt to give any description of the chaff. This term is a

loose one and includes two kinds of chaff, that which immediately encloses the grain (grain-chaff, palets) and that the glumes which subtends the grain with its grain-chaff. This distinction may be readily understood by a comparison of oat and wheat. In the oat the grain-chaff (palets) permanently invests the grain, so that after threshing, the "grain" consists of the grain proper plus its chaffy covering of two parts, one larger (outer palet) inclosing the grain, and the other smaller, (the inner palet). The grain of wheat, on the other hand, shells out of the grain-chaff, in which respect rye behaves similarly. Some varieties of barley are like the oat, differing only in the fact that the grain-chaff is firmly attached to the grain. (Harlan, 1918). The structure of these various kinds of chaff differs very widely, so that a full account of all the details would occupy much space. We may note particularly the thin papery character of the inner palet in wheat and rye. Inasmuch as the contribution of chaff to straw is in any event very small, such an account is unnecessary. At the same time, since a certain, if small, amount of chaff is bound to remain attached to straw, and hence may be found in paper, although in exceedingly small proportion, it is advisable to indicate the general character of the structures which may be found.

In addition to the chaff, the rachis or that portion of the steam which bears the grain, will contribute a similarly small proportion to straw pulp. The rachis presents equally special conditions of structure, and would call for much detail of description. For this reason also, the following summary of structural characters is confined to very general terms.

Barley. The chaff consists of slender loose parts (glumes) and the bead of the outer palet (lemma). Both palets would be included in straw of hulled varieties. Numerous very thick walled trichomes, strongly oblique in form, give the characteristic roughness of the head of barley. The trichomes of the inner or upper face of the beard are small and thin walled. Cells resembling crown cells occur near the base of the glumes. Crown cells occur locally in small numbers near the apex of the outer palet (lemma), which when adherent, contribute but little to pulp.

In all the cereals according to Hohnel (1875) the hypodermal cells (bast cells immediately beneath the epidermis) of the thick palets have teeth which articulate with corresponding depressions in the epidermal cell walls, and I have verified this. I have not found this condition in the beard.

Oat. Chaff consisting normally of glumes only. These are thin and leaf-like. The epidermal cell walls are wavy except in the thin papery marginal regions, the cells themselves much shorter than in the leaf. The bearded varieties will contribute trichome cells.

The palets of unfilled grain with of course an occasional filled grain will find their way into pulp. The epidermis is very sinuous and thick walled. There are a few crown cells, which are evidently undeveloped trichomes. They are distinct in appearance from those of wheat because of their somewhat irregular or oblique form. They are quite infrequent. Short, very thick walled trichomes on the outer palet and, along the fold of the inner palet, very numerous trichomes which can be distinguished by their lack of obliquity, standing out as they do at right angles (or nearly so) to the folded edge whence they spring.

Rye. Glumes and palets, with beard, constitute the chaff. The glumes and outer palet are similar in structure, characterized chiefly by large thick walled curved trichomes placed along the fold. The inner palet papery, the epidermal cells thin walled except toward the base, and thin walled crown cells numerous. These are readily distinguishable. The walls of the epidermal cells, especially those between the stomata very sinuous.

Wheat. Glumes and palets are the chaff. Very thick walled epidermis and trichomes characterize the glumes and outer palet. The thin papery margins of the inner palet has numerous rather slender trichomes arising from cells, which, as such, are very numerous and have the same appearance as those of the leaf.

The dwarf cells in all the foregoing generally consist as elsewhere of a larger crescentic thinner walled cell and a smaller very thick-walled cell. More exceptionally the dwarf cells occur singly, especially, for example, in the epidermis of the beard of barley. These do not in any event afford distinguishing characters.

It will thus be seen that crown cells, which would occur only in wheat straw pulp if the chaff were excluded, may otherwise be found also in oat and rye straw pulp. Even barley is not certainly excluded on this score. Trichomes, which would be found only in rye and wheat straw pulp, chaff excluded, may otherwise be found in all. The chief purpose of these additional notes therefor is to show the necessity of close study in the event that strict identification is desired.

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